The Absence of Sharks from Abyssal Regions of the World's Oceans.

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The oceanic abyss (depths >3000m), one of the largest environments on the planet, is characterized by absence of solar light, high pressures and remoteness from surface food supply necessitating special molecular, physiological, behavioral and ecological adaptations of organisms that live there. Sampling by trawl, baited hooks and cameras we show that the Chondrichthyes (sharks, rays and chimaeras) are absent from, or very rare in this region. Analysis of a global data set shows a trend of rapid disappearance of chondrichthyan species with depth when compared with bony fishes. Sharks, apparently well adapted to life at high pressures are conspicuous on slopes down to 2000m including scavenging at food falls such as dead whales. We propose that they are excluded from the abyss by high energy demand, including an oil-rich liver for buoyancy, which cannot be sustained in extreme oligotrophic conditions. Sharks are apparently confined to ca. 30% of the total ocean and distribution of many species is fragmented around sea mounts, ocean ridges and ocean margins. All

populations are therefore within reach of human fisheries, and there is no hidden reserve of chondrichthyan biomass or biodiversity in the deep sea. Sharks may be more vulnerable to over-exploitation than previously thought.

Keywords: Chondrichthyes, sharks, deep-sea fishes, abyss, elasmobranches,

1. INTRODUCTION.

The abyssal regions of the world's seas and oceans (depth >3000 m) have been colonised by fishes during the last 70Ma, contemporary with appearance of birds and mammals on land. This was enabled and is sustained by oxygenation of deep water by the modern global thermohaline circulation (Merrett & Haedrich,1997). Owing to stagnation events, final invasion of the eastern basins of the Mediterranean occurred only 6000 years ago (Rohling,1994). Deep-sea fishes were first discovered in the 1860s and Günther (1880) reported the deepest bony fish as *Gonostoma microdon* at 5300 m from the Pacific ocean whereas the deepest Chondrichthyes were a ray from 1033 m and a shark from 915 m. Deep-sea fishes are not a distinct taxonomic group but are derived from a diversity of shallow water types. Amongst the Chondrichthyes, including Holocephali (chimaeras) and Elasmobranchii (sharks and rays), many species show anatomical adaptations to deep sea life including eyes sensitive to low light levels and possession of light organs (e.g. *Isistius* spp.) (Widder, 1998). They now form an important component of deep-water fisheries down to 2000m depth (Gordon *et al.* 2003) and are conspicuous as scavengers at whale carcasses (Smith & Baco, 2003) and baited cameras (Priede & Bagley, 2000) suggesting that the deep sea may harbour a hidden diversity of Chondrichthyes.

All the major classes of vertebrates; mammals, birds, reptiles, amphibians, bony fish (Osteichthyes), and Chondrichthyes (sharks, rays and chimaeras) are suffering declines in species number and population sizes owing to habitat changes or exploitation (IUCN, 2004; Şekercioğlu *et al*, 2004). Chondrichthyes are almost entirely marine, whereas bony fishes are found in all aquatic environments from the highest altitude freshwater habitats through to the deep sea. Mammals, birds and reptiles occur in terrestrial, freshwater and marine environments and sperm whales *Physeter macrocephalus* are capable of diving (Wahlberg, 2002) to over 1000 m depth feeding on squid at bathyal depths. In comparison with the diversity of environments occupied by these other classes of vertebrates the Chondrichthyes are rather restricted in their habitat although mobility and world-wide distribution of many species make this a successful group.

From the earliest discoveries in the 19th century to the present day, records have consistently shown that Osteichthyes occur to much greater depths than Chondrichthyes. Nevertheless it has been argued that biological sampling of the deep ocean (ESM) remains inadequate and many species and populations of animals remain to be discovered. However if the depth distribution of Chondrichthyes is truncated at the boundary of the abyss, this has important implications for management and conservation of these species which are being heavily exploited throughout their global distribution (Baum *et al.* 2003; Stevens *et al*. 2000)

In this study we deployed sampling equipment to which both Chondrichthyes and Osteichthyes are susceptible over a depth range from less than 500 m on slopes and over mid ocean ridges to the abyssal plains at 4800 m in the Atlantic Ocean and 5900 m in the Pacific Ocean. Three different techniques were used, baited cameras, long-lines with baited hooks and demersal trawling. We combine this with an analysis of the cumulative historical record to examine the global depth limits of distribution of Chondrichthyes compared with the Osteichthyes.

2. METHODS.

(a) Trawling

A 45 foot (13.7 m) semi-balloon otter trawl (OTSB) was used. The trawl was shot on twin warps with 120 kg otter boards bridled to a single warp once the doors had spread (Merrett & Marshall, 1981). Nominal spread of the mouth of the trawl (width of sea-bed sampled) was 8.6 m. Haul duration was varied between a bottom contact time of 30min at the shallowest stations to 3 h on the abyssal plain and the tow speed was 2-2.5 knots. Sampling was done over a period of three years (2000-2002) during 5 cruises of the *RRS Discovery* in the NE Atlantic in the region of the Porcupine Sea-Bight and Porcupine Abyssal Plain. Cruises were in different seasons to avoid biasing of sampling in relation to any fish migrations that might occur (Priede *et al.* 2003).

(b) Baited hooks

Long-lining was done using the commercial vessel *MS Loran* which is fitted out as an autoliner. During 12 fishing days in July 2004, 61 baited long line sets were done on the Mid-Atlantic Ridge between 42°N and 55°N at depths from 450 m to 4300 m A total of 87500 baited hooks were deployed.

(c) Baited Camera

Baited cameras were deployed using a free-fall lander technique (Priede & Bagley 2000). A piece of bait (usually mackerel weighing *ca*. 0.5 kg) was deployed on the sea floor within the field of view of a downward looking video or time-lapse stills (film or digital) camera attached to a lander frame with an onboard computer, data storage, depth and current sensors. The lander was left on the sea floor for up to 12 h during which time images of fish approaching, consuming and departing from the bait were recorded. The system was recovered by acoustic command from the ship and images were down-loaded for analysis. Species were identified by reference to standard texts and comparison with voucher specimens captured in trawls. Definitive species names could not necessarily be allocated and cryptic species might not be separable from images alone. Therefore species counts in photographs can be regarded as minimum estimates. Data from 166 deployments are analysed (ESM).

(d) Archive Data.

Archive data for depth of occurrence of marine and brackish water fish were abstracted from global data sets available on FishBase (Froese & Pauly 2004). Original references were checked for the deepest species including all occurrences of Chondrichthyes deeper than 2500m. Dubious records where sampling gear traversed a wide depth range and depth of capture was uncertain were rejected. Records of maximum depth were accepted for 669 species of Chondrichthyes and 8691 species of Actinopterygii.

3. RESULTS

(a)Pelagic Species

Chondrichthyes, notably sharks, are found near the surface in the open waters throughout the world's oceans. Filter feeding planktivors clearly must swim near the surface where most of their food is found but maximum dive depths of 850m and over 1000m have been recorded for the basking shark (*Cetorhinus*) (Sims *et al.* 2003). Graham *et al.* (2005) recorded a dive of a whale shark (*Rhincodon*) to over 980 m in the Atlantic Ocean off Belize whereas studies around the Seychelles in the Indian Ocean (ESM) logged dives to over 1000m depth for 6 min but no deeper than 1500m. Pelagic predatory sharks also spend most time at shallow depths (Sundström *et al*. 2001) but we cannot exclude the possibility that occasional dives deeper than 1000m may occur. Discovery of the deeper-living megamouth shark (*Megachasma*) (Taylor *et al.* 1983) encouraged speculation on presence of new species of deep-water pelagic sharks but the depth of capture of the first specimen was 400m, Nelson *et al.* (1997) tracked one in coastal waters at depths down to 166 m and putative maximum depth for this species is cited as 1000 m (Froese & Pauly, 2004). We can find no evidence of any pelagic chondrichthyan living at depths greater than 1500 m.

(b) Demersal Species.

The deepest living Chondrichthyes are bottom-living species described as demersal, benthic. We have sampled them in three distinctive ways, trawling, baited hooks on long lines and baited cameras placed on the sea floor.

*Trawl Capture.*In the NE Atlantic Ocean, west of Ireland, we carried out 52 bottom trawls at depths from 750 to 4800m (Figure 1) and found no Chondrichthyes in 17 trawls deeper than 2500m depth. In contrast, the deepest trawl (4835 m) returned 8 species of bony fish (Actinopterygii). In a series of 17 trawls on the Mid-Atlantic Ridge at 930-3505m we found no Chondrichthyes deeper than 2520m except for one holocephalan, *Harriota* spp. at 3010m.

Long Lines. In a survey of the Mid Atlantic Ridge in 61 baited long line sets at 433 to 4200m. The deepest Chondrichthyes below 3000 m, were a ray, *Bathyraja pallida* and a shark, *Centrophorus squamosus* both captured at 3280 m. *Bathyraja richardsoni, Hydrolagus affinis* and *Etmopterus princeps* were caught at 2909 m and *Hydrolagus pallidus* at 2650m and *Dipturus batis* at 2619 m. Three deeper line sets caught no Chondrichthyes whereas bony fish were caught at all depths (Figure 2). All depths given are the minima for lines which may follow the bottom slope over 100-200m of depth amplitude.

Baited Cameras. We have collated data from 166 deployments of baited cameras placed on the sea floor at depths from 471m to 5900 m in the Atlantic Ocean at latitudes 53°N-54°S (Armstrong *et al.* 1992; Priede *et al.* 1994; Collins *et al.* 1999), the North Pacific Ocean (Priede & Smith 1986, Priede *et al.* 1990, Priede *et al*. 1994), Indian Ocean (Witte 1999) and Mediterranean Sea (Jones *et al.* 2003). Of 84 deployments at depths >2500m no Chondrichthyes were found (Figure 3) except for observations of rays at 2630m in the Porcupine Sea Bight (NE Atlantic), and at 2908m and 3396m on the slopes of the Mid Atlantic Ridge. The deepest sharks were *Hexanchus griseus* and *Etmopterus spinax* at 2490m in the Mediterranean Sea. The deepest chimaera was at 2355m on the Mid-Atlantic Ridge. Osteichthyes were present at all depths.

Archive Data With the exception of 7 species, Chondrichthyes were confined to depths less than 2500 m (Figure 4). Two Holocephali were reported to occur to 2600 m, the Rhinochimaeridae *Harriotta haeckeli* and *Harriotta raleighana* (Last & Stevens 1994). The deepest sharks were *Isistius brasiliensis* reported from the surface to 3500 m (Compagno *et al.* 1995) and *Centroscymnus coelolepis* reported to 3700m (Forster 1973) and observed from a submersible at 3690 m depth (Clark & Kristof, 1990). The ray *Rajella bigelowi* is probably the deepest chondrichthyan fish described as "Benthic on deeper continental slopes and probably abyssal plains between 650 and 4156m" (Stehman 1990). Thus, while Chondrichthyes are largely confined to depths less than 2500m, 260 species of bony fish from several families were reported from depths greater than 2500m. The deepest recorded fish was the cuskeel *Abyssobrotula galatheae* trawled from 8370m (Nielson, 1977).

Grouping the species into 500m depth bins we have plotted the number of species as a function of their maximum depth (Figure 5). For Chondrichthyes the slope of decrease in species number with depth was 0.8 log units (630%) per 1000m compared with only 0.4 log units (250%) per 1000m for Actinopterygii. This indicated a much more rapid disappearance of Chondrichthyes with depth than the bony fish.

4. DISCUSSION.

Recent data from a number studies using depth sensing devices attached to sharks indicate that pelagic species are found no deeper than 1500m in the open ocean. On continental slopes, around islands, seamounts and on the mid ocean ridges bottom-living or demersal Chondrichthyes were found down to 3000m and with rare occurrences down to just over 4000m. Numerous trawl and baited camera samples on the abyssal plains never revealed the presence of any Chondrichthyes. The Beebe project using deep-diving manned submersibles concluded that sharks may not normally inhabit waters deeper than 2128 m but found rays and chimaeras at greater depths and indicated that more research is needed to reveal to true depth ranges (Clark & Kristof, 1990). In the present study except for one recorded capture, sharks were absent from all samples deeper than 3000 m, whereas bony fish were found at all depths. We believe the case is already clear that Chondrichthyes have generally failed to colonise the oceans deeper than 3000 m and it is very unlikely that major new populations will be discovered in abyssal regions.

The data presented in figures 4 and 5 are the maximum recorded depths for each species and do not represent typical depth of distribution. We conclude that the cumulative sampling effort over almost 150 years since the first discovery of the deep sea ichthyofauna has now accurately delineated the maximum depth limits for the chondricthyes as essentially absent from the abyss at depths >3000m. Extrapolation of the lines of maximum depth in Figure 5 gives a theoretical maximum depth for the deepest chondrichthyan of 3893m. For bony fish the corresponding depth of deepest occurrence is 8350m; very close to the actual depth of capture of the *Abyssobrotula galatheae.*

(a) ***Volume of Ocean Occupied by Chondrichthyes***

The total volume of the oceans is 1.37×10^9 km^3. Assuming that pelagic Chondrichthyes occur everywhere to a depth of 1500 m, and demersal species down to 4000m and up to 250m off the bottom, the ocean volume used by Chondrichthyes is 0.395×10^9 km^3. (Figure 6). Hence over 70% of the global ocean volume is devoid of Chondrichthyes which are confined to the surface layers, ocean margin regions, around ocean islands, mid ocean ridges and sea mounts. These areas are all intensively fished and there is no evidence of a deep refuge of chondrichthyan biodiversity or biomass in the abyss. Defining the abyss as depths of 3-6 km (Herring 2002), Chondrichthyes are essentially absent from this and the hadal zone >6 km. Furthermore we hypothesise that the abyssal plains may represent barriers to migration and dispersal (especially given the lack of planktonic stages in Chondrichthyes) although such movement cannot be excluded on the basis of existing evidence.

(b) Explaining the Absence of Chondrichthyes from the Abyss.

Any hypothesis explaining the absence of Chondrichthyes from the abyss should take into account the fact that many species are well adapted to the deep-sea conditions at 2-3000 m. For example chimaeras are generally cold-water deep sea fish absent from shallow waters less than 80 m depth, abundant in the 1000-2000 m depth range but never found in the abyss.

*Species Number***.** In both bony fish and Chondrichthyes, species number decreases with depth (Figure 5). Simple probability implies that the bony fish are more likely to have produced representatives capable of surviving in deep environments by virtue of much higher species number in shallow water, rather than any underlying physical, physiological or ecological cause. However it is evident that species number declines much more rapidly in Chondrichthyes and the lower species reservoir in shallow water does not explain lack of representation in the abyss. If Chondrichthyes had the same species extinction rate with depth as the Actinopterygii we would expect their maximum depth to be 7500 m permitting survival throughout the abyssal regions of the world and into the margins of the hadal trench systems.

*Body size***.** There is considerable debate regarding body size trends in fish across depth strata in the oceans. A study of trends in bony fish size between 500 and 5000 m depth in the NE Atlantic shows that scavenging species are bigger deeper whereas there is no significant size trend in non-scavengers. Metabolic modelling of foraging strategies shows a clear advantage of increased size of scavengers in the oligotrophic environment of the abyss (Collins *et al.* 2005). It is evident from Figure 4 that Chondrichthyes are predominantly bigger fish than Actinopterygii. Since many Chondrichthyes can function as scavengers and are attracted to bait this would suggest a possible advantage for their survival in the abyss. It is paradoxical therefore to observe that it is the Chondrichthyes with their larger size that show a higher extinction rate with depth. Abstracting large Actinopterygii (>29cm max. length, spanning the same size range as the Chondrichthyes) from the global data base the number of species decreases at a rate of 0.4 log units per 1000m; the same as for all Actinopterygii (Figure 5). Compared with Actinopterygii, Chondrichthyes are clearly deficient in their ability to survive at increasing depth and this has precluded their colonisation of the abyss.

*Water temperature***.** The deep sea is cold with typical temperatures of 2-4°C but it is very unlikely that such temperatures exclude Chondrichthyes from the abyss. There is no sharp temperature discontinuity at the upper boundary of the abyss and many species of fish are capable of living within this temperature range. This does not exclude the possibility that the presence of intermediate water masses such as the Mediterranean intermediate water in the North East Atlantic might act as an environmental cue enabling deep slope-dwelling species to orientate to an optimum depth. The influence of temperature as a barrier to colonisation of the abyss is however further excluded by the observation that Chondrichthyes are also absent from the abyssal Mediterranean sea where we have observed sharks attracted to baits at depths down to 2490 m and only Actinopterygii present at greater depths (Jones *et al.* 2003). The Mediterranean Sea is warm all the way to the bottom (ESM). It is evident that Chondrichthyes are excluded from abyssal regions of the seas independently of the prevailing temperature regime.

Hydrostatic pressure. To preserve cellular function at high pressure, deep sea organisms require; homeoviscous adaptation of membranes, and structural adaptation of proteins (Macdonald, 2001). These effects are evident in bony fish species living deeper than 1000m and whilst there are no data for Chondrichthyes, we presume that pressure tolerance is well developed in this group. Furthermore Chondrichthyes generally have high concentrations of trimethylamine *N*-oxide in their body fluids. In addition to acting as an osmolyte, TMAO has been shown to act as a universal stabiliser of protein structure. The muscles of deep sea shrimps, agnatha, Chondrichthyes and Osteichthyes all have increased concentrations of TMAO compared with shallow water species apparently conferring pressure tolerance on structural and enzyme proteins (Yancey *et al.* 2002). With generally high TMAO concentrations it seems that Chondrichthyes are pre-adapted to life at high pressures. Since many species of Chondrichthyes can survive at 2000-3000 m depth, and there are occasional records to over 4000 m it is unlikely that there is a fundamental physiological barrier to this group extending its distribution to 6000 m, a modest proportional change in pressure.

Buoyancy. A characteristic of the deep water sharks is large livers, rich in lipids that enable them to attain almost neutral buoyancy. Probably the most successful demersal scavenging and predatory fish in the abyss is *Coryphaenoides (Nematonurus) armatus* (Actinopterygii, Macrouridae) which uses a gas-filled bladder for buoyancy. For 1 kg of buoyancy using squalene (specific gravity 0.86) requires 7.14 kg of oil with an energy content 264 MJ. The same buoyancy using a gas-filled bladder entails a theoretical pumping cost at 4000m depth of 90 kJ, calculated for oxygen (ESM). Even assuming efficiency of 5-10%, the energy cost of buoyancy using an air bladder is trivial compared with a lipid based system, making incremental increases in buoyancy during growth much less expensive assuming the swim bladder wall is gas impermeable. For shallow-water fish adjusting the quantity of gas in the swim bladder during vertical movements can be energetically costly but for abyssal fish such movements, since they are a small proportion of total water depth, result in negligible volume changes and there is no requirement to adjust quantity of gas in the bladder. Once the bladder is inflated, given low permeability of the swim bladder wall, maintenance cost of the swim bladder in abyssal fish is lower than for shallower living species making the same absolute vertical movements.

Metabolism. Studies of swimming speed (Collins *et al.* 1999) and metabolism (Bailey *et al.* 2002) in bathyal (1000-3000 m) and abyssal fish species indicate much lower activity in the latter linked to a decrease in food supply with depth. We believe the proximal reason for absence of Chondrichthyes from the abyss is the absence of truly low energy forms for survival in a deep oligotrophic environment. The penalty of the need for a large lipid-rich liver may be decisive in excluding Chondrichthyes from the abyss. The complete lack of "whole-animal" or tissue metabolic rate studies leave this as an open question, which certainly demands further investigation.

Reproduction. Chondrichthyes have direct life cycles without larval stages reproducing either through hatching of small adult forms from egg cases (Stehman & Merrett 2001) or through bearing of live young. Such miniature adults may be vulnerable in the abyss and some species migrate into shallower water to breed. Many deep-water bony fishes however produce buoyant eggs and larvae that are presumed to develop remote from the sea floor and benefit from greater food supply at surface layers of the oceans (Merrett & Headrich, 1997).

5. CONCLUSIONS

Observations or captures of Chondrichthyes at depths over 4000 m are very rare whereas at these depths bony fishes and other fauna can be quite abundant. The deepest confirmed reports of a shark *Centroscymnus coelolepis* at 3700 m and the ray *Rajella bigelowi* at 4156 m are both species with their main zone of distribution at much shallower depths; minimum depths are 270 m, 650 m and respectively. This is in contrast to a number of bony fishes that have minimum depths in excess of 3000 m. The world's deepest fish, *Abyssobrotula galatheae* has a minimum depth of 3110 m and *Coryphaenoides yaquinae* which is an abundant macrourid on the abyssal floor of the Pacific Ocean seen in our baited camera images at 5900 m (Figure 3) has a minimum depth of 3400 m (Froese & Pauly 2004). Discovery of a new shark, ray or chimaera at depths greater than 3000m with its predominant distribution in the abyss is very unlikely. Special expeditions to reveal such a fauna may be difficult to justify but as research expands in the deep sea more of the ocean will be surveyed and gradually certainty regarding faunal composition of the abyss will increase.

There is probably no single simple explanation for the absence of Chondrichthyes from the abyss. More research is needed on the effects of pressure on metabolic enzyme activity, membrane structure and adaptations to pressure in Chondrichthyes. Most information that is available is for bony fishes.

The Chondrichthyes and sharks in particular are threatened world-wide by the intensity of human fishing activity. The finding that they are largely absent from regions of the deep sea beyond the reach of commercial fisheries further emphasises concern regarding the conservation of this class of vertebrates. Owing to low productivity and slow growth rates in the deep sea, exploitation of deep water species is generally of doubtful sustainability. However some of the Actinopterygii that are captured commercially have a depth distribution beyond the maximum depth of economically viable fisheries. For example the roundnose grenadier *Coryphaenoides rupestris* with a fishery targeted at shoals 500-1000m deep, occurs down to 2200m.

There is no such deep "protected area" for Chondrichthyes, and the whole Class may potentially be at risk.

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Figure Legends

Figure 1. North East Atlantic Ocean, numbers of species captured in trawls at different depths. Grey symbols- Actinopterygii, Black Symbols – Chondrichthyes

Figure 2. Mid Atlantic ridge, numbers of species captured in trawls at different depths. Grey symbols- Actinopterygii, Black Symbols - Chondrichthyes.

Figure 3. Number of species of fish attracted within view baited cameras deployed at different depths, Atlantic, Pacific, Indian Oceans and Mediterranean Sea. Grey symbols- Actinopterygii, Black Symbols – Chondrichthyes, Horizontal line at 3000m indicates the upper limit of the abyss.

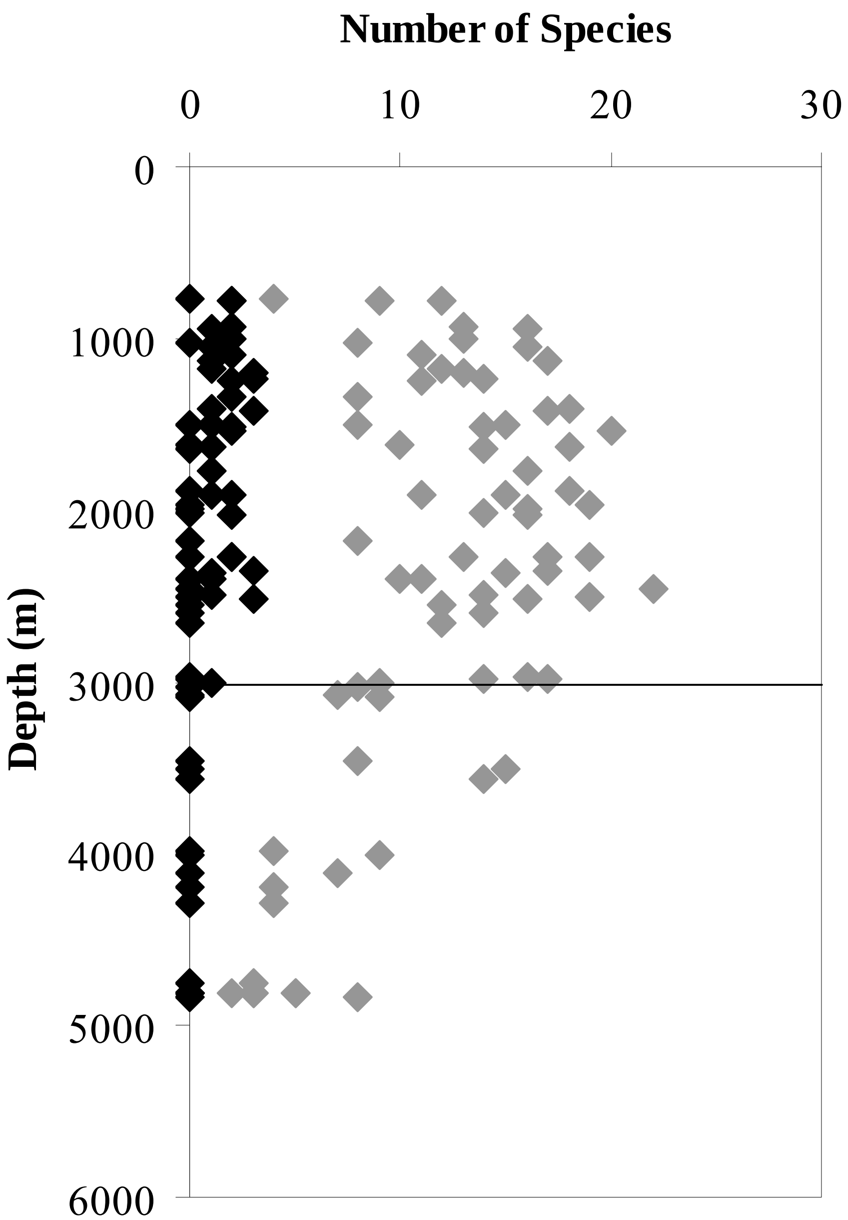
Figure 4. Maximum depth of occurence of Chondrichthyes and Actinopterygii. Global data set for maximum adult total body length and depths of 669 species of Chondrichthyes (Black Symbols) and 8691 species of Actinopterygii (Grey Symbols).

Figure 5. Rates of decrease in species numbers with depth. Log_{10} of number of species depth maxima per 500m stratum for the global data set. Black symbols and line – Chondrichthyes ($Log_{10}N = -0.0008x + 2.9969$, $r^2 = 0.992$),
Grey symbols and line – Actinopterygii ($Log_{10}N = -0.0004x + 3.3227$, $r^2 = 0.9375$),
Open Symbols and thin line – Large Actinopterygii corresponding to the size range of the Chondrichthyes ($Log_{10}N = -0.0004x + 2.9733$ $r^2 = 0.9176$).

Figure 6. The volume of ocean occupied by chondricthyes. A hypsographic diagram showing the “chondrichthyan” volume in black. Apart from possible absence from the extreme depths of the hadal ocean trenches (>9000m depth) the Actinopterygii can be assumed to occur throughout the ocean volume (grey)

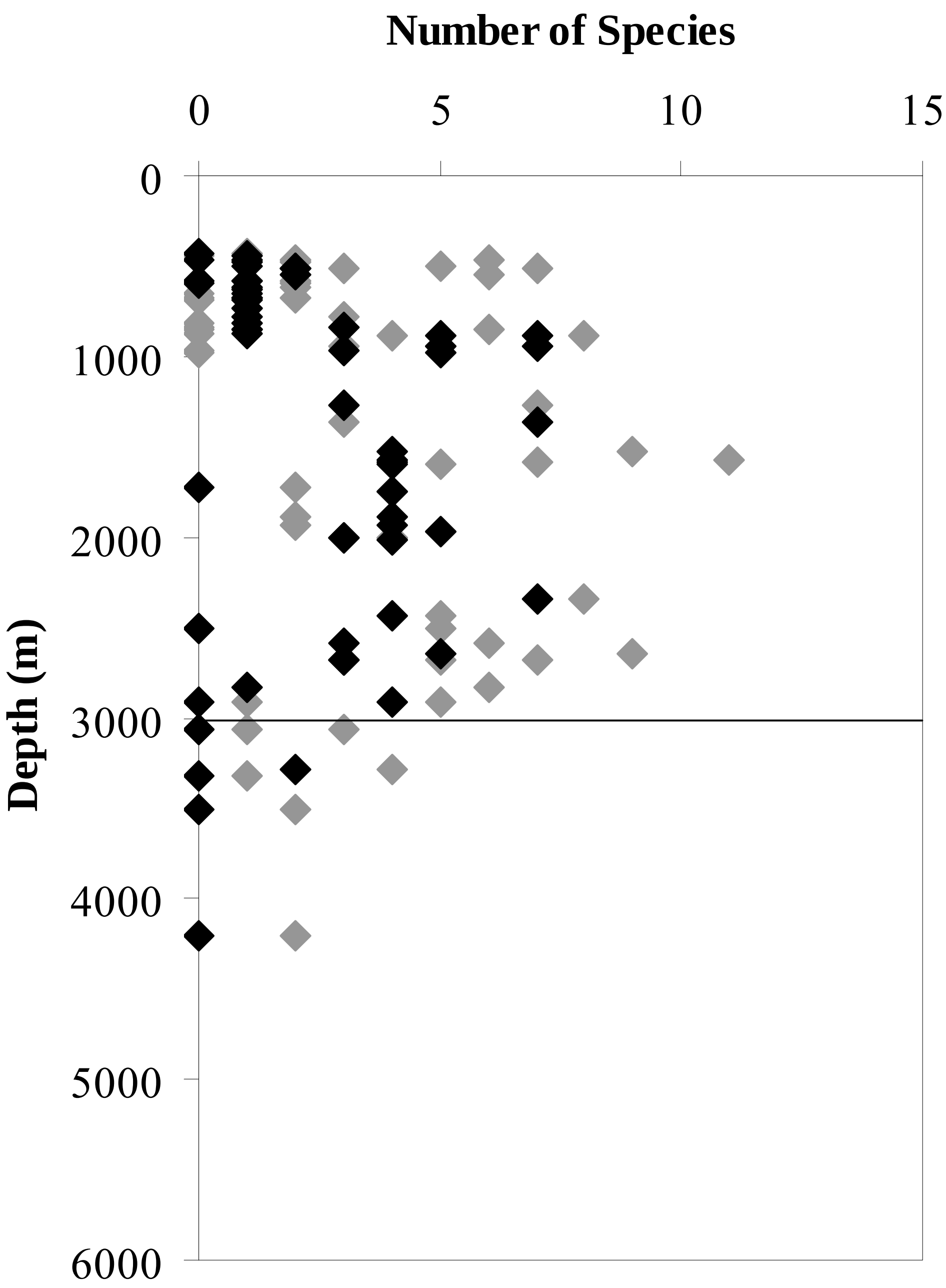
Short Title: Absence of Sharks in the Abyss

FIGURE 1



Number of Species
0
10
20
30
0
1000
2000
3000
4000
5000
6000
Depth (m)

FIGURE 2



Number of Species
0
5
10
15
0
1000
2000
3000
4000
5000
6000
Depth (m)

FIGURE 3

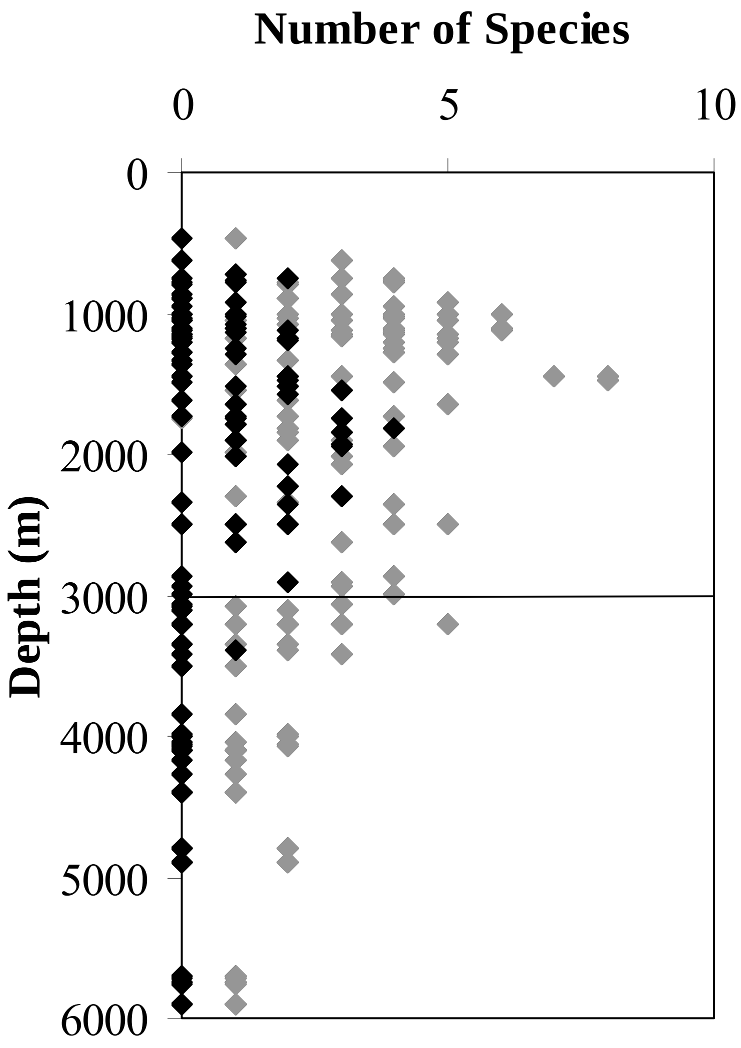
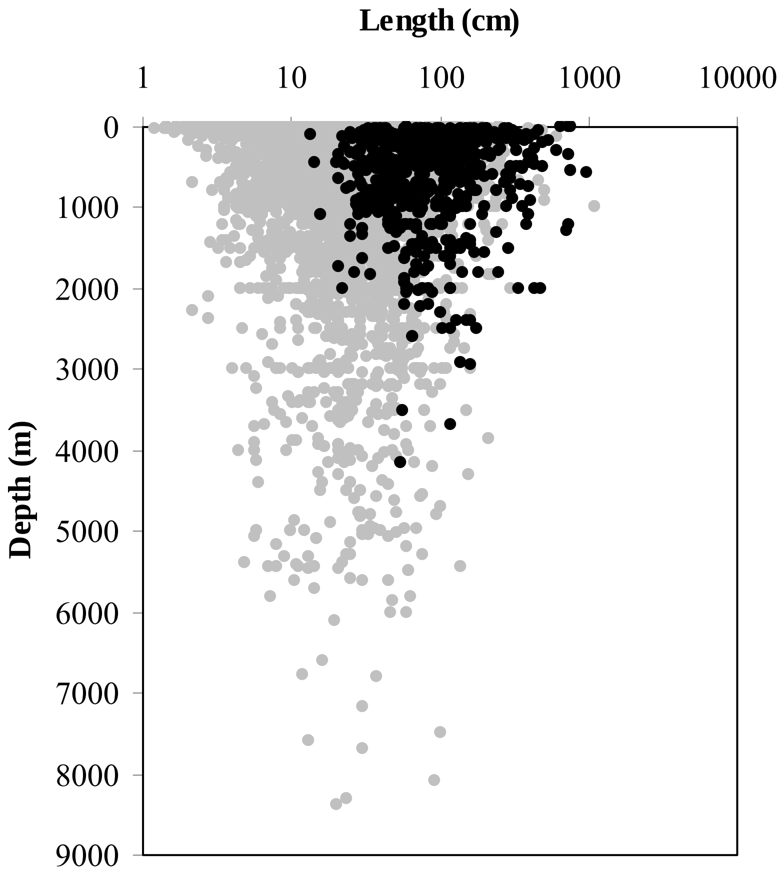

Number of Species
0
5
10
0
1000
2000
3000
4000
5000
6000
Depth (m)

FIGURE 4



Length (cm)
1
10
100
1000
10000
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
Depth (m)

FIGURE 5

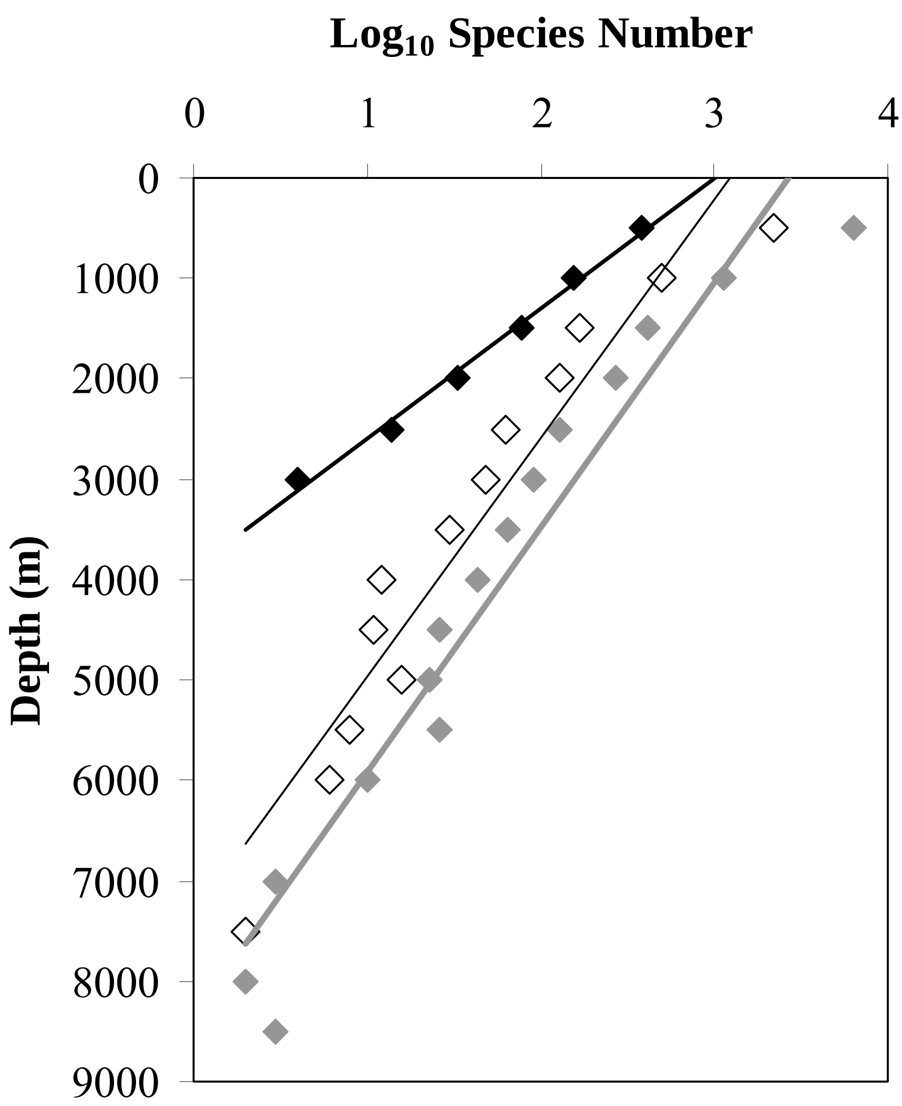
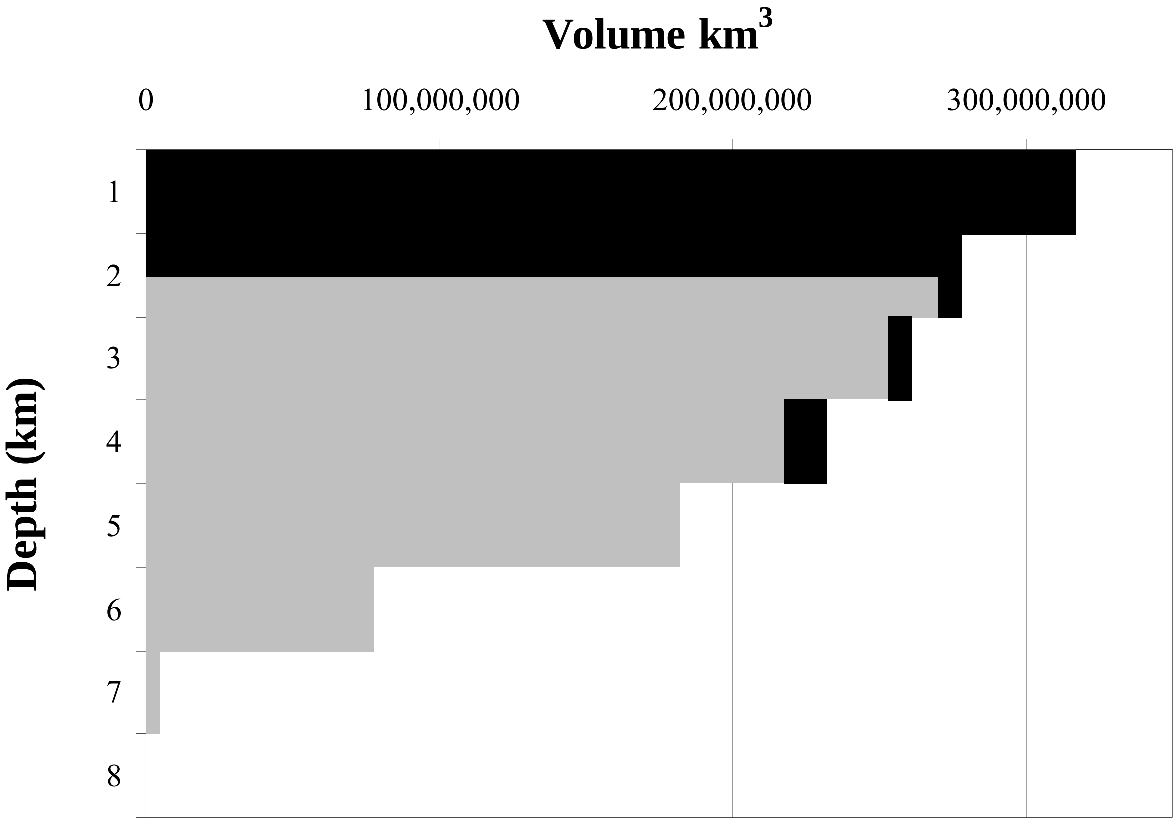

Log$_{10}$ Species Number
0
1
2
3
4
Depth (m)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000

FIGURE 6



Volume km3
0
100,000,000
200,000,000
300,000,000
1
2
3
4
5
6
7
8
Depth (km)